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Exotic species drive patterns of plant species diversity in 93 restored tallgrass prairies

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Abstract

A primary goal of restoration ecology is to understand the factors that generate variability in species diversity and composition among restorations. Plant communities may assemble deterministically toward a common community type, or they may assemble stochastically, ending differently because of weather conditions during establishment, soil legacy effects, or exotic species propagule pressure. To test these alternative hypotheses, we sampled plant communities and soil at 93 randomly selected restored prairies distributed throughout Iowa, USA. Five remnant sites were sampled as a reference. We tested our hypotheses using multiple regressions and investigated the strength of direct and indirect effects on species diversity and richness using structural equation models. The prairie restorations were highly variable in their age, size, diversity, soil characteristics, and how they were managed post-seeding. The strongest predictor of plant species richness and diversity was the degree of invasion, as measured by the abundance of exotic species. Restorations planted with species-rich seed mixes had reduced exotic species abundance, which led indirectly to higher species richness of restorations. Sites with higher organic matter and a more linear shape had a direct positive effect on exotic abundance, which in turn decreased diversity. We found little support for deterministic assembly, and diversity did not increase with the age of planting. Our results indicate that restored prairie communities tend to assemble into states of high or low diversity, driven by invasion from exotic plant species. Management of exotic species is essential for maximizing species diversity in temperate grassland restorations.

Keywords

grassland, invasive species, prairie, restoration, plants, tallgrass

Disciplines

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Comments

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Exotic species drive patterns of plant species diversity in 93 restored tallgrass prairies

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Abstract. A primary goal of restoration ecology is to understand the factors that generate variability in species diversity and composition among restorations. Plant communities may assemble deterministically toward a common community type, or they may assemble stochastically, ending differently because of weather conditions during establishment, soil legacy effects, or exotic species propagule pressure. To test these alternative hypotheses, we sampled plant communities and soil at 93 randomly selected restored prairies distributed throughout Iowa, USA. Five remnant sites were sampled as a reference. We tested our hypotheses using multiple regressions and investigated the strength of direct and indirect effects on species diversity and richness using structural equation models. The prairie restorations were highly variable in their age, size, diversity, soil characteristics, and how they were managed post-seeding. The strongest predictor of plant species richness and diversity was the degree of invasion, as measured by the abundance of exotic species. Restorations planted with species-rich seed mixes had reduced exotic species abundance, which led indirectly to higher species richness of restorations. Sites with higher organic matter and a more linear shape had a direct positive effect on exotic abundance, which in turn decreased diversity. We found little support for deterministic assembly, and diversity did not increase with the age of planting. Our results indicate that restored prairie communities tend to assemble into states of high or low diversity, driven by invasion from exotic plant species. Management of exotic species is essential for maximizing species diversity in temperate grassland restorations.

Key words: *grassland; invasive species; prairie; restoration; plants; tallgrass.*

Introduction

A fundamental question in restoration ecology is whether the full biodiversity represented in reference areas can be achieved in restored areas, given enough time (Bradshaw 1987). Biodiversity is a key integrative measure that has been linked to higher ecosystem functions in grasslands, including productivity, nitrogen mineralization, and litter decomposition (Hooper et al. 2005, Isbell et al. 2011). It is also positively associated with stability, especially the consistency of biomass production across years (Tilman et al. 2001, 2006, Isbell et al. 2009), and resistance to extreme precipitation events (Isbell et al. 2015). Biodiversity is also important to pollinators in grasslands, because animal-pollinated forbs are more abundant in more diverse sites (Haddad et al. 2001). Remnant prairies can have 15–20 species in areas <0.5 m^2 (Pärtel and Zobel 1999, Martin et al. 2005, Polley et al. 2005), and restoring this high diversity remains a challenge. The factors that are responsible for reproducing this high diversity in restorations remain understudied (Symstad and Jonas 2011).

Two theories make distinct predictions on how species assemble into diverse communities over time during restoration (reviewed by Temperton and Hobbs 2004). The deterministic model predicts that communities will assemble toward a predictable and consistent community composition and diversity over time as determined by local environmental conditions. Many restoration seed mixes include later successional species at establishment to overcome dispersal limitation and bypass the early colonization stage by design. Under the deterministic model, the composition of the seed mix, time, and local environmental conditions would be the most important variables for predicting restoration outcomes, with diversity generally expected to increase over time as species recruit from the mix (Fig. 1; Wilsey and Martin 2015). However, few studies have tested this assumption, and some find that diversity peaks after a few years and then declines over time as tall grasses dominate (Pimm 1991, Sluis 2002, Grman et al. 2013).

The stochastic/alternate state model predicts that factors that are somewhat random set the trajectory of community development, which can lead to alternate

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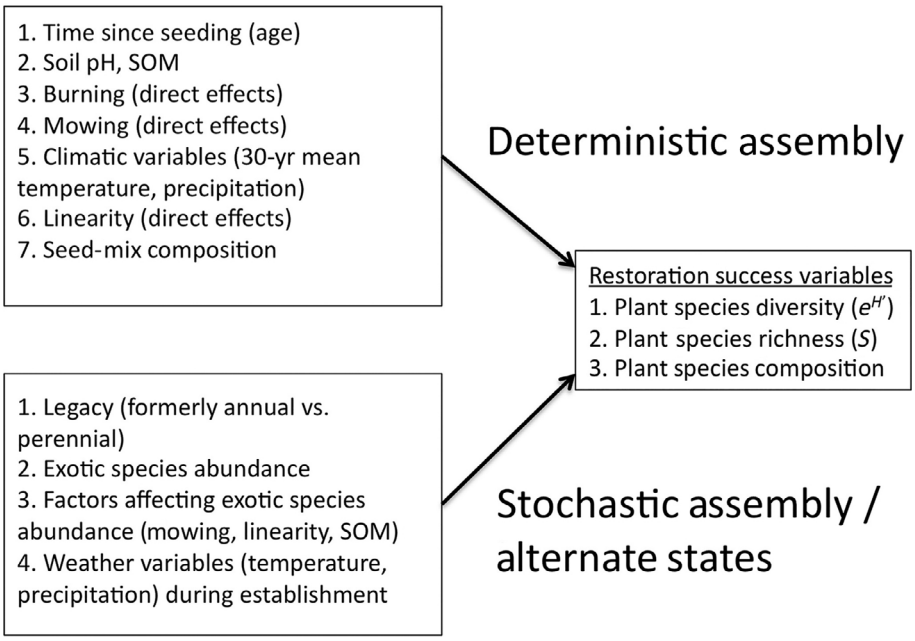

FIG. 1. Conceptual relationships between community assembly models and predictors of restoration outcomes in prairie grasslands. Soil organic matter is abbreviated as SOM.

compositions. For example, weather during initial years post-seeding can lead to unpredictable outcomes if conditions are far from the climatic norm (Manning and Baer 2018, Groves and Brudvig 2019), and compositions that form during this time can have long-term impacts through priority effects. Soil legacy or priority effects can have strong influences on assembly, resulting in different species diversities and compositions even when seed mixes and environmental conditions are similar (Temperton and Hobbs 2004, Martin and Wilsey 2012). Restoration compositions that differ between sites that were formerly annual crop fields vs. pastures, or among sites that differed in their exotic species propagule pressure, would support the stochastic/alternate states model. High perennial exotic species abundance has been found to be strongly associated with reduced prairie species establishment and diversity (Martin and Wilsey 2012, 2014), but it remains poorly known when and if exotic species affect species diversity overall (Wardle et al. 2011). Ecosystems can lose native species and gain exotic species, but when these processes occur simultaneously, the net change in richness, diversity, and function may be neutral, positive, or negative, depending on the abundance of exotics and how their traits differ from species they replaced (Wardle et al. 2011).

Species diversity can be partitioned into spatial components of alpha, beta, and gamma, where alpha is a measure of average local diversity, beta diversity is the spatial turnover in species, and gamma is total diversity (Whittaker 1960, Anderson et al. 2011). Beta diversity is less well studied than alpha but has been found to be affected by species sorting along abiotic gradients, dispersal, variation in assembly history (Questad and Foster 2008, Martin and Wilsey 2012), and actions by animals such as urine deposition or grazing (Steinauer and Collins 1995, Loreau 2000, Chase 2003, Soininen et al. 2007, Martin and Wilsey 2015). Restoring beta diversity is extremely important for grassland restoration, as higher beta diversity in restored tallgrass prairies has been linked to higher ecosystem multifunctionality (Grman et al. 2018).

Patterns of within-site beta diversity may change over time during ecological restoration, but this has seldom been tested. In early years, beta diversity is expected to be low, since seeds generally are homogenously distributed throughout the site. Deterministic assembly predicts that over time, beta diversity should increase due to species sorting along environmental gradients (Faber and Markham 2011). The increase in beta diversity in turn could affect site level (gamma) diversity. Alternately, the presence of exotic species could influence patterns in beta diversity, and exotics could lower beta diversity over time if they disperse throughout and homogenize the site (Loreau 2000, Martin and Wilsey 2015). Based on these mechanisms, we predict that within-site beta diversity will increase with site age when exotics are rare but will decrease with age when exotics are abundant.

An unresolved question in grassland restoration is how management actions and site characteristics affect restoration success (Grman et al. 2015, Norland et al. 2015, Larson et al. 2018). Most studies that have

compared grassland restorations have focused on a single mechanism, have been conducted at a single location, or have not randomly sampled both successful and unsuccessful restorations in a random manner. Contrasting variably successful restorations can be used to compare the roles of seed mix, management, and site characteristics on restoration success (Ewel 1987, Suding 2011). Tallgrass prairie restorations allow for testing community assembly processes in the absence of dispersal limitation for late-successional species because restored prairies are an example of active restoration, where diverse seed mixes are seeded on to bare ground.

Here, we test for relationships between measures of restoration success (plant diversity and similarity of restorations to their seed mixes) and predictor variables in a large number of randomly selected tallgrass prairie restorations in the central United States. Restoration success was evaluated across 93 restorations, and compared to five remnant prairies. We tested the following alternate hypotheses, (1) restoration success measures (site-level and beta diversity [richness and effective species number], target species establishment, and similarity to remnants) increase with age and are associated with environmental variables (Fig. 1), (2) these restoration success measures do not increase with age but are more strongly predicted by variables associated with the stochastic/alternate state mode of community assembly (e.g., weather, past land use history, and the abundance of exotic species, Fig. 1), and (3) management actions significantly influence restoration success.

Methods

Study system and site selection

We sampled restorations within the tallgrass prairie region of the central United States. The tallgrass prairie is a temperate sub-humid grassland, characterized by long-lived perennial plants, Mollisol soils with high organic matter, a deep alpha horizon, and high annual productivity. Remnant tallgrass prairies have very high alpha diversity and richness, with 15–20 species occurring in less than 0.5 m^2 (Martin et al. 2005, Polley et al. 2005). Restorations in this area benefit by having access to the most diverse commercially available seed for any system (White et al. 2018). Precipitation in Iowa is highest in the south and southeast (mean 965 mm), and decreases substantially toward the north and northwest (mean 660 mm).

We randomly selected 93 restored conservation and roadside prairies across the state of Iowa for sampling. We sampled 44 during 2015 and 49 during 2016. A random sampling approach was used to obtain an unbiased sample of restorations. We randomly selected conservation restorations from Iowa Department of Natural Resource (DNR) sites, and included four additional county- or university-owned sites. We randomly selected prairie restorations established by the DNR out of a GIS database of 1,314 restorations in which native grasses and forbs were planted. For roadside restorations, we selected sites from among the hundreds of restorations around the state of Iowa by selecting a subset of Iowa counties, randomly selecting a location on the county map, and then sampling the nearest restoration to that point. We excluded counties in the loess hills region of western Iowa because they are less generally representative of the tallgrass prairie region. Only sites that were seeded with both prairie grasses and forbs, and that were not over-seeded into intact vegetation, were included. None of these sites were grazed by bison or cattle. No restorations were immediately adjacent to remnants. Sites varied widely in quality and management. The 93 sites used in our analysis were from 27 counties in Iowa and were located across the four largest Iowa landforms, excluding the Loess Hills and riparian flood plains (Fig. 2). Of the 93 total sites, 46 were roadsides restorations and 47 were "conservation" restorations, of which 43 were managed by the DNR and four were managed by other public entities.

Five remnant prairies (never plowed, heavily grazed by cattle, or seeded) in the Iowa preserve system were also sampled to provide a benchmark for establishment success. Two remnant prairies (Cayler and Liska-Stanek) were sampled in July 2015, and three more, (Doolittle, Marietta, and Anderson/Dyas) were sampled in July 2016. These remnants were selected to represent variability among prairies in the state ranging from clay to sandy soil types.

Sampling design

A sampling approach was used that could quickly assess the composition and diversity of plants of a given site in order to be able to visit a greater number of sites overall. All sampling was done in July to ensure a full canopy had developed but still capture most early-season species. At each site, we used point-intercept sampling to estimate cover and the number of species. We dropped a 20 × 50 cm quadrat containing four pins at 10–25 random locations within each site to sample plants (Martin et al. 2014, Martin and Wilsey 2015). The number of sampling locations per site varied with area of the site (although species richness was rarified to standardize on number of locations). At each restoration, the identity and number of species present was noted at each sample location, and the number of point contacts was recorded by species. All hits were recorded (i.e., multiple hits per pin were possible) to account for layering and to ensure that number of hits was as closely related to biomass as possible (Wilsey et al. 2011, Xu et al. 2015). This provided information on percent cover of target species (species in the original seed mix) and volunteer native and exotic species (species not native to Midwestern North America).

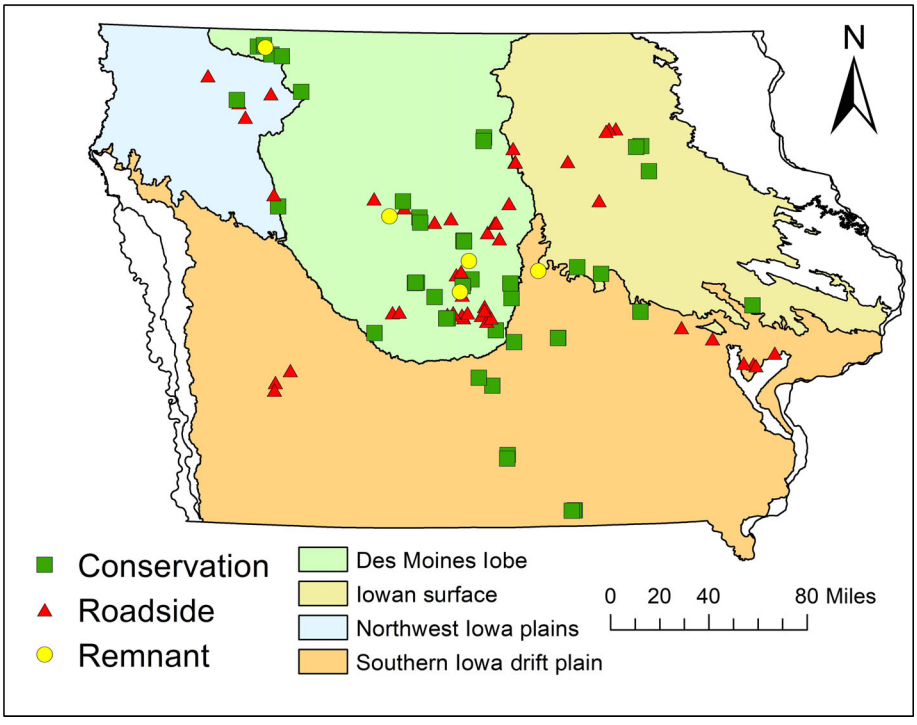

FIG. 2. Map of sampled locations with respect to major landforms. 1 mile = 1.61 km.

Management and site characteristics

At each site, we collected three soil cores (2.5 cm diameter and to 10 cm depth) from which we measured soil bulk density (g/mL), pH, and organic matter. Soil bulk density provides an estimate of soil compaction, which is expected to be an important predictor of establishment success (Heneghan et al. 2008). Soil pH is a strong indicator of soil history and includes the effects of past management (e.g., the amount of nitrogen fertilization and liming) (Silvertown 1980). Organic matter is an indicator of soil fertility, water availability, and landscape position, with greater organic matter in lower elevation hydric sites compared to xeric hilltop sites (Burke et al. 1989, Honeycutt et al. 1990, Barrett and Burke 2000).

After sampling the sites, we surveyed managers about the history and management of each restoration. We obtained information on the year the prairie was planted, species that were seeded, method used in seeding, when any burn or mowing (cutting and leaving biomass) occurred, land use prior to seeding with prairie species, and if any other management actions occurred. We were unable to collect information for all variables at all sites because records were not always available or bulk seed mixes were used. We obtained lists of species in the seed mix for 66 sites, of which 48 indicated the relative abundances of seed sown for each species. We did not know the exact age of the restoration planting at seven sites. Sites were categorized into three groups based on mowing frequency: none (n = 34 sites), establishment (n = 31 sites), or other (n = 28 sites). The "none" category classified restorations that were never mowed after being seeded. The "establishment" category described sites that were mowed at least one time in the first 2 yr after the restoration date. The "other" category combined sites where the mowing treatment was unknown or it was known to receive a mowing treatment different than the sites that were only mowed during establishment. Examples of these other treatments are haying (cut and remove cut biomass) and being mowed only after the first 2 yr. We classified burn treatments into four categories: none (n = 43), once (n = 16), multiple (n = 27), and unknown (n = 7). Using survey responses about the history of the site prior to restoration, we grouped sites into three land-use classes: perennial (n = 50), crops (n = 33), or unknown (n = 10). The "perennial" category included sites in roadsides, pastures, or set aside from farming in the U.S. Conservation Reserve Program, previously dominated by perennial plant species. The "crops" category includes all previous land use in row crops, which would likely have a seed bank of mostly annual species. To examine the effect of the seeding method, we grouped treatments into four categories: broadcasted (n = 46), drilled (n = 31), combination (n = 6), or unknown (n = 10). The "broadcasted" treatment included hand broadcasting, mechanized dry broadcast seeders, and hydro-seeders. The "combination" treatment was for sites planted with both a seed drill and some form of broadcast seeding.

We acquired climate and establishment weather data from the United States NOAA National Climatic Data Center (NCDC), accessed February 2020. Climate norms (30-yr averages from 1981 to 2010) and individual yearly values of mean annual temperature and precipitation were downloaded for the weather station nearest to each site. For each site, establishment weather corresponded to mean temperature and precipitation over the first 2 yr after seeding, or the first year for one-year-old restorations, at the nearest weather station where data were available.

Data processing

Estimates of species diversity were quantified with species richness and Shannon's diversity ($e^{H'}$, or effective species number), calculated at the site level. We calculated these measures using all species, and for native species only, and these two measures were highly correlated with one another ($r = 0.91$). Total species richness and diversity were also partitioned into alpha and beta components to test hypotheses about beta as described below. Richness (total number of species) was standardized across sites by rarefaction to 10 quadrats per site with EcoSim700 software (Gotelli and Entsminger 2001). Because 10 quadrats was the minimum sampling effort used among all sites, we can rarefy richness in sites with a greater sampling effort (25 quadrats maximum; average 15.3) to produce comparable measures of richness across restorations. Shannon's index was not rarified because it is independent of sampling effort above very small values of N (Lande 1996).

Beta diversity was estimated within sites for both rarefied total species richness and effective species number, using the multiplicative model, where $\beta = \gamma/$ mean α. Based on the typology of Anderson et al. (2011), we are interested in non-directional variation in beta diversity within sites, and we are specifically interested in comparing variation in beta diversity among a priori groups of invaded vs. less-invaded grasslands. To test our prediction that beta diversity increases with site age when exotics are rare, but decreases when they are abundant, we classified sites as either being more-invaded with above average (>50% of abundance being exotic species), or less-invaded with below average (<50%) exotic species abundance.

We calculated the average number of hits per quadrat (summing four pin drops) from exotic species at each site and used this as a measure of invasion. We used a perimeter/area ratio to measure site linearity, where a line has a ratio of 2 and a square has a ratio of 1. We calculated linearity using a measure of fractal dimension, with the equation linearity = 2ln(perimeter/4)/ln(area) (Olsen et al. 1993, Frohn 1998). Thus, more linear habitats, with a higher ratio of perimeter to area and more edge effects have a higher ratio (closer to 2).

Plant community data were used to calculate the following restoration success variables: site-level and beta species richness and effective number of species, native species richness alone, floristic quality index, and compositional relatedness between seed mixes and restorations (Bray-Curtis similarity). Similarity measures between the seed mix (pure live seed mass) and the sampled community used all species combined, and only seeded species. We calculated a floristic quality index as $FQI = -c\sqrt{s}$, where s is total richness and c is a coefficient of conservatism for each species for the state of Iowa, which is designated by local botanists (Wilhelm et al. 1999). Coefficient of conservatism is an expert-derived estimate of how restricted species might be to "high quality" remnant areas.

Statistical analyses

Continuous predictor variables (Table 1) were regressed against response variables with multiple regression approaches, then the smaller set of significant predictor variables were included as covariates in models with categorical variables (management treatments, site type, and previous land use). For the first step, we used general linear models with stepwise selection and Mallows $C(p)$ statistic as the selection criterion (Proc GLM Select in SAS 9.4; SAS Institute, Cary, North Carolina, USA) and evaluated significance ($\alpha < 0.15$) of each variable with type III sums of squares. To prevent problems of autocorrelation among variables, soil bulk density and ln(area) were not included because they were correlated with soil organic matter ($r = -0.61$), and linearity ($r = -0.60$), respectively. The perimeter/area (linearity) measure was used instead of area because it is has mechanistic implications and area is incorporated into its formula. For the second step, we tested the effect of categorical management variables (seed method, burn treatment, mow treatment), site type (roadside vs. conservation planting), and previous land use (legacy) as fixed effects in an ANCOVA to understand their effects while accounting for the significant continuous predictor variables. We used a priori contrasts to test hypotheses about the effects of categorical management variables on plant species richness and diversity. We tested whether diversity was higher with establishment mowing vs. no mowing treatment, since mowing may suppress annual weeds that establish before the target species and reduce establishment from the mix. Contrasts compared cropped vs. perennial legacy, burned vs. unburned prairies, and restorations burned multiple times vs. just once.

We compared remnant and restored prairies using t-tests (Proc TTest in SAS 9.4), testing whether they differed in species diversity, richness, abundance of exotic species, proportional abundance of graminoids, and floristic quality (FQI).

We tested our prediction that beta diversity will increase with site age using an ANCOVA, which compared slopes of beta diversity–age regressions between invaded and non-invaded restorations using Proc GLM in SAS 9.4. A significant interaction between the effect

TABLE 1. Summary of site characteristics in 93 tallgrass prairie restorations.

Variable	*N*	Mean	SD	Range
Continuous predictor variables				
Age (yr)	86	10	6.0	1–26
Site size (ha)	93	5.4	10.8	0.14–61.04
Linearity	93	1.18	0.14	1.00–1.55
Soil pH	93	7.4	0.6	6.03–8.17
Soil bulk density (g/cm^3)	93	1.3	0.2	0.92–1.93
Soil organic matter (%)	93	9.5	2.8	3.61–17.40
Annual precipitation average (mm)	93	902.8	57.5	729.2–974.1
Annual temperature average (°C)	93	8.8	0.9	7.17–10.72
Establishment precipitation (mm)	82	885.2	146.2	609.2–1,241.3
Establishment temperature (°C)	82	9.0	1.38	5.94–12.25
Exotic species abundance	93	13.41	7.92	0.04–28.90
Seed mix variables				
Seeded richness	66	37.8	19.8	7–81
Seeded diversity ($e^{H'}$)	48	11.6	4.4	4.12–23.16
Graminoid (% mass of pure live seed)	48	76.3	10.3	57.23–99.05
Response variables in restorations				
Species richness	93	21.0	6.85	4.00–35.98
Species richness (natives only)	92	13.9	5.84	2.60–27.28
Diversity (Shannon's $e^{H'}$)	93	9.12	4.85	1.24–23
Floristic quality index	93	10.48	5.01	0.87–21.09
Proportion graminoid	93	0.68	0.18	0.13–0.99
Compositional similarity between seed mixes and restoration				
All species	48	0.18	0.17	0.00–0.68
Seeded species only	48	0.28	0.20	0.00–0.73

of age and invaded status on beta diversity or beta richness would support the hypothesis that beta is developing differently over time in invaded vs. less invaded sites. Beta diversity was also regressed against exotic species abundance and tested with polynomial regression, testing for linear and quadratic effects.

We used structural equation models to test hypotheses about direct and indirect effects of continuous measured variables using Proc CALIS in SAS 9.4, using a confirmatory approach. We tested whether higher seed-mix richness and diversity resulted in more diverse restorations through direct effects or indirectly through its effects on exotics. Specifically, we tested the predictions that species diversity measures increased directly with the diversity of the seed mix, or indirectly through seed-mix diversity effects on exotic species. We included the proportional abundance of graminoids in these models, because the effect of dominant grasses on the degree of invasion or recruitment of species from the mix may be important. Proportional graminoid abundance was not significantly correlated with seed mix richness ($r = -0.18$) or seed-mix diversity ($r = 0.15$). Preliminary analyses suggested that exotic species were important in predicting restoration success, so we developed SEMs to test for direct effects of age, linearity, and soil organic matter on diversity vs. their indirect effects on diversity through their effects on exotic species abundance. We developed a prediction a priori that edge effects and higher soil fertility would favor exotic species, and that this, in turn, would indirectly influence plant diversity and richness. T-scores were used to evaluate significance and were calculated as $\hat{\beta}/\hat{\sigma}$ where $\hat{\beta}$ is an estimated path coefficient, and $\hat{\sigma}$ is the standard error associated with that estimate. Standardized effect scores (r) are reported in all figures and text. All models presented are saturated and have perfect fit by definition (Grace 2006).

RESULTS

We found variation in management practices and site characteristics for all of the predictor variables (Table 1). Variation in predictor variables is a requirement for meaningful regression models. Age of the restorations averaged 10 yr and ranged from 1 to 26 yr old, capturing the full age range of most tallgrass prairie restorations (Table 1). The number of species in the seed mixes averaged 38, with a range of 7–81 species. Site area averaged 5.4 ha and ranged from <1 to >60 ha. Sites varied in their annual precipitation amounts and were located on soils over several Iowan landforms (Fig. 2).

Comparisons of restorations to remnants

On average, restorations differed significantly from remnants in species diversity and composition. Restorations had 39% of the Shannon's diversity ($t_{96} = 6.43$, $P < 0.001$) and 49% of the species richness ($t_{96} = 6.85$, $P < 0.001$) of remnants (Table 1). We sampled restorations with extremely low diversity (5% of remnant levels) and more diverse sites that approached, and in one case exceeded the average diversity of the five remnants we sampled. In restorations, exotic species abundance ranged from 0–98% of all hits, with an average of 50% abundance, making them about twice as invaded as the remnants ($t_{15.6} = -9.76, P < 0.001$). Restorations were also more graminoid-dominated than remnants (means 68% vs. 52%, $t_{25.42} = -7.00, P < 0.001$). Restorations had significantly lower average FQI (mean = 10.5) than remnant prairies (mean = 23.5; $t_{96} = 5.6, P < 0.001$).

Predictors of site-level species diversity and richness in restorations

When evaluating environmental predictors of restoration success, exotic species abundance was, by far, the strongest predictor of species richness and Shannon's diversity across restorations (Table 2, Fig. 3). Exotic

species abundance was strongly negatively correlated with the diversity and richness of restorations (Fig. 3). This was found whether the analysis was based on all species or only native species sampled (Table 2). Other variables tested were nonsignificant. Age of restoration was not significantly related to the diversity, total richness, or native richness of the restoration (i.e., their diversities did not increase over time, $P > 0.15$; Appendix S1: Fig. S1 A–C).

Among the management variables, mowing was the strongest predictor of both total and native species richness. Richness was significantly higher in sites mowed during establishment than sites that were never mowed or received other mowing treatments ($P = 0.011$ Table 3, Fig. 4). Mowing did not significantly affect Shannon's diversity. Total richness was higher in roadsides than conservation areas after accounting for other variables in the model. Seeding method significantly affected richness of native species, with restorations seeded using a combination of broadcast and drilled seed having more native species than restorations seeded with a single method (Table 3). Burn treatment and prior land use were not significant (Table 3).

Environmental predictors primarily affected diversity and richness through their indirect effects on exotic species abundance, rather than through direct effects. Our SEM indicated that linear and more fertile habitats had higher exotic abundance, which in turn suppressed plant species diversity (Fig. 5; Appendix S1: Table S1).

Effect of seed mixes on diversity of restorations

Seed mix variables had significant effects on richness and diversity in the restorations, but significance was due to their indirect effects on exotic species abundance (Fig. 6; Appendix S1: Table S2). Seed-mix richness was negatively correlated with exotic species abundance ($r = -0.430$), which in turn was negatively correlated with restoration richness ($r = -0.631$). Thus, the indirect effect of seed richness on richness of the restoration was positive ($r = -0.430 \times -0.631 = 0.271$). Somewhat surprisingly, the diversity of the seed mix was positively associated with exotic species abundance ($r = +0.585$), which in turn, was negatively associated with diversity of the restorations ($r = -0.616$). Thus, the overall effect of the diversity of the seed mix was different than that of mix richness, having a net negative effect on diversity of the restorations ($r = +0.585 \times -0.616 = -0.360$). Neither species richness, nor diversity of seed mixes directly affected the species richness or diversity of restorations (Fig. 6a).

Beta diversity and richness

Abundance of exotic species also affected beta diversity and richness, but not in the manner that we predicted. Exotic species abundance had a nonlinear relationship with beta diversity, with drops in beta diversity only occurring at high levels of exotic abundance and beta richness increased linearly with exotic abundance (Fig. 7b, d). Neither beta richness nor beta diversity changed significantly over time in restorations (Fig. 7a, c). Invaded sites (over 50% exotic abundance) had lower beta diversity ($F_{1,82} = 6.29$; $P = 0.014$) than less invaded sites (Fig. 7a). Conversely, there was a trend of higher beta richness in invaded sites, but this difference was not significant ($F_{1,82} = 6.29$; $P = 0.067$).

Predictors of species composition

Exotic species abundance was also a predictor of target species establishment (similarity in species

Table 2. Multiple regression results from analyses of 93 tallgrass prairie restorations.

	Species richness						Compositional similarity			
	Diversity ($e_{H'}$); $N = 82$, $R^2 = 0.30$, df = 1,81		All species; $N = 82$, $R^2 = 0.27$, df = 1,81		Natives only; $N = 81$, $R^2 = 0.44$, df = 1,80		All species; $N = 44$, $R^2 = 0.71$, df = 1,43		Seeded species only; $N = 44$, $R^2 = 0.47$, df = 1,43	
Factor	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*
Exotic species abundance	<0.01	34.5	<0.01	29.4	<0.01	62.22	<0.01	39.88	0.03	5.21
Linearity	>0.15		>0.15		>0.15		<0.01	14.67	<0.01	18.24
Age	>0.15		>0.15		>0.15		>0.15		>0.15	
Precipitation (establishment)	>0.15		>0.15		>0.15		<0.01	11.66	<0.01	10.17
Temperature (establishment)	>0.15		>0.15		>0.15		>0.15		>0.15	
Precipitation (normals)	>0.15		>0.15		>0.15		>0.15		>0.15	
Temperature (normals)	>0.15		>0.15		>0.15		>0.15		>0.15	
Soil organic matter	>0.15		>0.15		>0.15		>0.15		>0.15	
Soil pH	>0.15		>0.15		>0.15		>0.15		>0.15	

Notes: Effects of environmental variables (soil OM, pH), weather during establishment (temperature and precipitation during the first 2 yr of establishment), and site characteristics (linearity and age of restoration) on species diversity, species richness (rarified), and Bray-Curtis similarity between communities sampled and seed mixes. Bray-Curtis used all species, or only species in seed mixes (seeded only). *F* values and *P* values are not provided in final model using stepwise selection, but as noted variables with $P > 0.15$ were excluded.

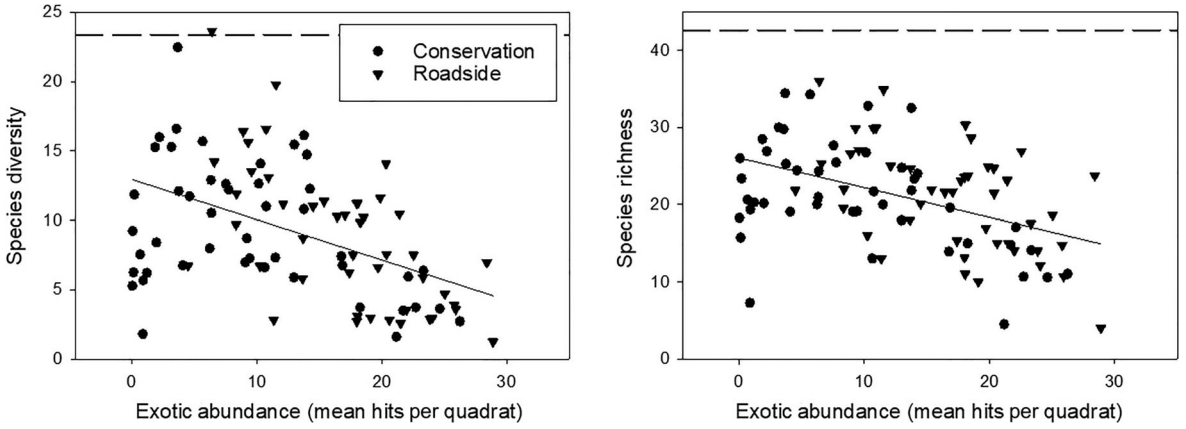

FIG. 3. Relationships between species diversity (Shannon's $e^{H'}$, left) and richness (right) and abundance of exotic biomass. The dashed lines show the mean diversity and richness of the five remnants.

TABLE 3. ANCOVA results from a sampling of 93 tallgrass prairie restorations.

	Species richness							Bray-Curtis similarity				
	Shannon's diversity; $N = 93$, $R^2 = 0.352$		All species; $N = 93$, $R^2 = 0.382$		Native species; $N = 92$, $R^2 = 0.552$			All species; $N = 44$, $R^2 = 0.788$		Seeded species; $N = 44$, $R^2 = 0.690$		
Factor	*P*	*F*	*P*	*F*	*P*	*F*	df	*P*	*F*	*P*	*F*	df
Deterministic predictors												
Seeding type	0.407	0.98	0.249	1.40	0.034	3.04	3	0.168	1.80	0.662	0.53	3
Burning	0.870	0.24	0.432	0.93	0.330	1.16	3	0.788	0.24	0.225	1.56	3
Linearity								0.751	0.10	0.197	1.73	1
Stochastic predictors												
Exotic species abundance	<.001	28.96	<.001	23.94	<.001	51.77	1	0.001	15.45	0.085	3.16	1
Site type	0.076	3.22	0.033	4.71	0.239	1.41	1	0.092	3.01	0.010	7.48	1
Prior land use	0.095	2.43	0.463	0.78	0.290	1.26	2					
Precipitation during establishment								0.047	4.25	0.041	4.53	1
Mowing	0.155	1.91	0.021	4.08	0.018	4.24	2	0.516	0.68	0.605	0.51	2
Contrasts												
Mow: none vs. establishment	0.093	2.88	0.010	6.98	0.010	6.91	1	0.987	0.00	0.592	0.29	1
Seeding type: drill vs. broadcast					0.108	2.64	1					
Seeding type: combination vs. one					0.027	5.10	1					
Error df							79					32

Notes: Effects of deterministic and stochastic/alternate state predictors of diversity and composition (see Fig. 1). Bray-Curtis similarity measures how similar the sampled community was to the seed mix. Bray-Curtis seeded is a measure of similarity between the seed mix and the seeded species in the community. Degrees of freedom were lower for Bray-Curtis measures because many sites used a bulk seed mix or did not know the exact species composition of seed mixes. Only significant covariates (Table 2) for each response variable were included in these models.

composition between seed mixes and restorations). Similarity between seed mixes and restorations was significantly lower in restorations with higher exotic species abundance (Table 3, $P < 0.001$). However, this effect was only nearing significance when considering seeded species only ($P = 0.085$). Precipitation during the establishment years was the next best predictor of compositional similarity, such that restorations with higher precipitation had higher similarity measures (Tables 2 and 3). When considering only seeded species, restorations had higher similarity to their mixes in conservation areas compared to roadsides (Table 3). Age of restoration was unrelated to its compositional similarity to its seed mix or to its floristic quality index ($P > 0.15$, Appendix S1: Fig. S1D).

DISCUSSION

The 93 prairie restorations we sampled were highly variable in their site characteristics, management, and

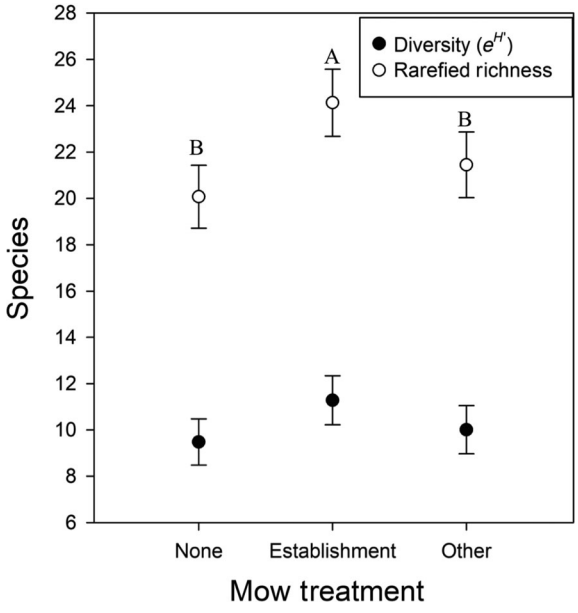

FIG. 4. Species diversity and richness of restorations with no mowing, mowing during establishment (first 2 yr), or "other" (mostly unknown mowing frequency or mowing after establishment years). Diversity was significantly higher with mowing during establishment than the other two treatments.

similarity to a remnant community. Two sites out of 93 achieved the high diversity of remnants, but most were much less diverse. We found that the abundance of exotic species was the most important predictor of species diversity and native and total richness. Seed mix variables affected diversity through their indirect effects on exotic abundance. Exotic species were more abundant in sites with higher soil organic matter and that were more linear in shape, leading to reduced diversity and richness. Mowing was the most important management variable, with sites that were mowed during establishment having higher native and total species richness than un-mowed sites. Taken together, these results were most consistent with a stochastic model of community assembly (Fig. 1). Our results were not consistent with the deterministic model because diversity was neither significantly related to restoration age, soil characteristics, or climate, nor directly affected by seed-mix composition.

Effects of exotic species

Consistent with the stochastic/alternate state model for community assembly, our results indicate that abundance of exotic species is the best predictor of our diversity-focused measures of prairie establishment success. Sites can vary in their exotic species abundance due to their past history or management. Exotic species can establish quickly and can suppress native species establishment from seed (Yurkonis et al. 2010, Dickson et al. 2012, Wilsey et al. 2015).

In ecological restoration, exotic species are often assumed to arrive early following disturbance and subsequently drop out of the community due to exclusion from competitively dominant native species (Camill et al. 2004). This is most applicable to annual exotics that disperse readily and grow quickly. However, the three exotic species we sampled most frequently were the perennial grasses *Bromus inermis*, *Poa pratensis*, and *Phalaris arundinacea*. Other common exotics were perennial legumes, including *Lotus corniculatus*, *Trifolium pratense*, and *Securigera varia*. The most common exotic forbs were *Melilotus* spp., *Daucus carota*, *Pastinaca sativa* (biennials), and *Cirsium arvense*, a perennial. Therefore, in these perennial grasslands, the dominant exotics are not annuals, and we found that they can maintain their abundance for many years. Moreover, rather than adding diversity to the planted native community (Stohlgren et al. 1999, Cleland et al. 2004), exotic species in these restorations decreased diversity overall.

Exotic species dominance could lead to low diversity communities because exotics are ecologically different

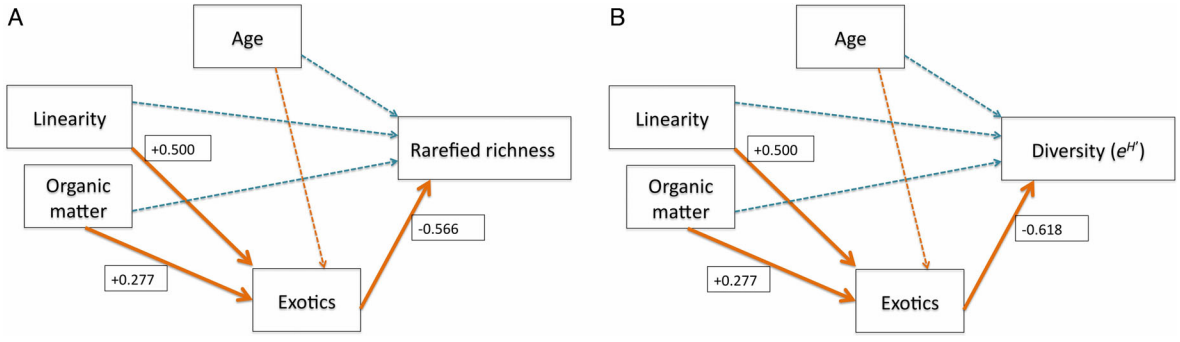

FIG. 5. Structural equation model exploring relationships between predictors of (A) richness and (B) plant diversity of prairie restorations. Age is the age of restoration, linearity is a measure of fractal dimension, and organic matter is a measure of soil fertility. Significant pathways are marked with a solid line, and nonsignificant ones are shown with dotted lines. Effect estimates (numbers in boxes) are standardized. Interactions supporting deterministic assembly are shown in blue, and stochastic assembly pathways are shown in orange.

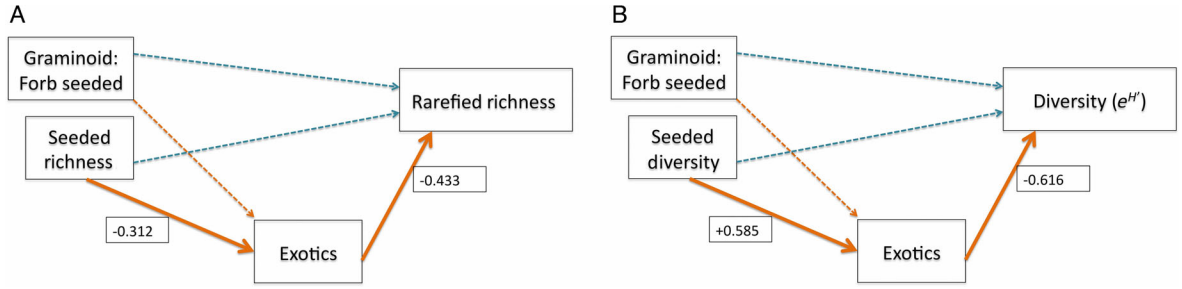

FIG. 6. Structural equation model exploring effects of seed-mix richness, diversity, and proportion of graminoids in the mix on prairie restoration (A) richness and (B) diversity. Effect estimates (numbers in boxes) are standardized. Significant pathways are marked with a solid line, and nonsignificant ones are shown with dotted lines. Interactions supporting deterministic assembly are shown in blue, and stochastic assembly pathways are shown in orange.

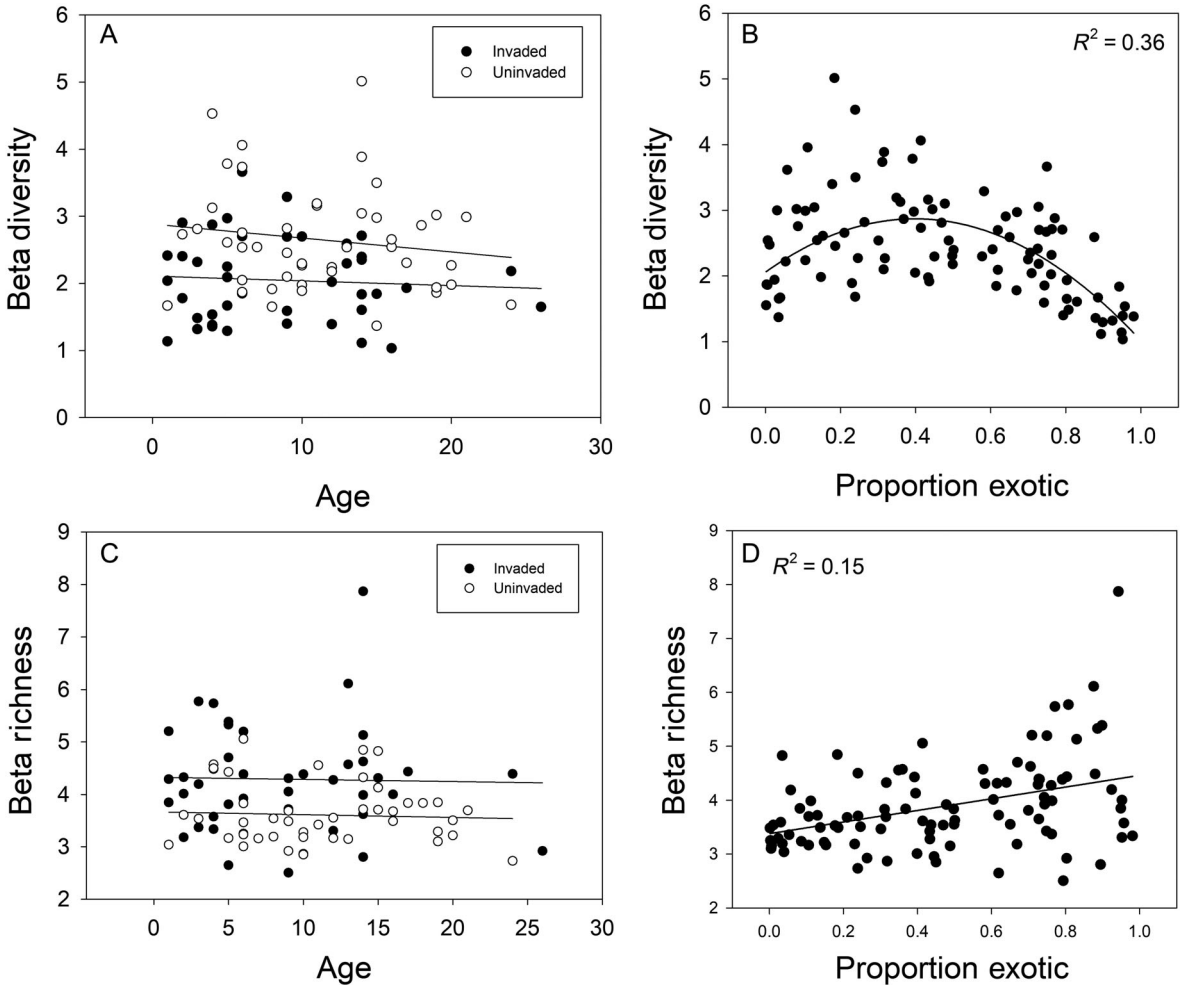

FIG. 7. Beta diversity and richness vs. (A, C) age of planting and (B, D) as a function of the amount of exotic species abundance across 93 restored prairies. "Invaded" sites in left panels have above average exotic abundance (>50%), whereas, less-invaded sites have lower than average exotic abundance.

than native species in several important ways. Exotics often have higher germination rates and emerge from soil earlier than comparable native species (Wilsey et al. 2015), have leaf trait values such as specific leaf area, leaf dry matter and N content that are more on the acquisition end of the leaf economics spectrum than

natives (van Kleunen et al. 2010), and can have stronger priority effects than native species (Dickson et al. 2012, Wilsey et al. 2015). Across the tallgrass prairie region, exotic-dominated grasslands have lower diversities and altered phenologies compared to native-dominated grasslands (Wolkovich and Cleland 2011, Martin et al. 2014, Wilsey et al. 2018). Exotics grow earlier in the spring, before the natives start to green up, and then later in the fall after natives have senesced (Wolkovich and Cleland 2011, Wainwright et al. 2012, Wilsey et al. 2018). These differences may be important aspects of exotic invasion into prairie restorations, since invasibility of prairie has been shown to be dependent on the phenological traits of the existing community (Losure et al. 2007). Once perennial exotic species become established, they are persistent (Kulmatiski 2006, Norland et al. 2015) and generally resist colonization from native species (Kulmatiski 2006, Dickson et al. 2012, Martin and Wilsey 2014).

We found evidence that soil organic matter and edge effects indirectly reduce diversity through effects on the degree of invasion. Organic matter is related to nitrogen availability, so its effect on exotic species may result from greater soil N, which tends to favor the acquisition-biased economics of exotic species (van Kleunen et al. 2010). In an experimental context, soil N reduction has been shown to promote greater native species establishment in restorations (Blumenthal et al. 2003). Organic matter is also highly correlated with topographical landscape position in grasslands, which results in differences in both nutrient and water availability (Burke et al. 1989, Jenny 1994). Exotic species have been shown to establish from the edge of remnant grasslands, with exotic abundance positively related to edge proximity (Cilliers et al. 2008).

Effect of mowing on diversity

Mowing during the first one or two growing seasons after a prairie has been seeded (establishment mowing) has been suggested to increase establishment of target species (Kurtz 1994), and it has become a commonly used tool in restorations (Rowe 2010). Our results support this practice, as it significantly increased both native and total species richness of restorations. Mowing can influence vegetation by creating above- or belowground gaps for new seedling establishment (Peltzer and Wilson 2001) and can reduce annual species by preventing them from setting seed. Mowing treatments are sometimes applied after establishment to continue suppressing exotic species that may grow earlier in the season than most natives. Future studies should investigate establishment mowing effects in greater detail, particularly how they affect annual vs. perennial exotics.

Lack of a relationship between site age and diversity

Under the deterministic assembly model, restored prairies should accumulate diversity over time, recruiting more species from the initial mix due to interannual variation in biotic and abiotic conditions and differences in species dormancy. However, we found no evidence that species diversity or richness were increasing with age of restorations. Previous work has shown that after initial recruitment and establishment, restored prairies often decrease or are stable in their richness and diversity (McLachlan and Knispel 2005, reviewed in Wilsey 2018). Decreases over time in other studies have been widely attributed to increasing C_4 grass dominance (Camill et al. 2004). We did not detect a significant change over time, even after taking into account variation in sown richness and the degree of invasion. Additionally, we didn't find any support for the prediction that FQI increases with restoration age, independent of total diversity or richness.

Beta diversity

We did not find evidence supporting our predictions that beta diversity would increase over time in less invaded sites, and decrease over time in invaded sites. We did find evidence that within-site beta diversity was higher in native-dominated than exotic-dominated restorations, consistent with the sampling of sites from Minnesota to Texas by Martin and Wilsey (2015). This may be driven in our sites by the abundance of *Bromus inermis*, which has been shown to reduce diversity in northern prairies by homogenizing plant communities within and across grasslands (Stotz et al. 2019). These results are inconsistent with a deterministic model of assembly, wherein beta diversity is predicted to increase over time through environmental sorting.

Effects of seed mixes

We found support that the seed-mix designs alter restoration outcomes (Sheley and Half 2006, Piper et al. 2007). Grman et al. (2015) found evidence that species sown at higher densities are more likely to establish (see also Larson et al. 2018). However, in contrast to these earlier studies, we found that the number of species in the seed mix had mostly indirect effects. Seed mixes with higher richness were associated with lower abundance of exotic species, and this in turn led to an indirect increase in the species richness of the restoration. In experiments that vary species richness, diverse plots tend to have fewer invaders than plots that are less diverse (Kennedy et al. 2002, Losure et al. 2007). Although we do not have direct, causal evidence, our results add to this body of literature and indicate that seed mixes with a greater number of species have important effects on restorations, often by suppressing exotic species establishment.

The graminoid to forb ratio in the seed mix may also influence restored plant diversity (Dickson and Busby 2009). Our results indicate that managers have generally sown mixes with high graminoid content. However, we did not find that the proportional mass of graminoids in

the seed mix significantly predicted richness or diversity after accounting for seeded richness or diversity, at least under the range of values studied here. Recommendations on optimal grass: forb ratios vary widely, but because the remnants we sampled had an average of 52% graminoid abundance, we recommend using a 1:1 ratio of forb to graminoid seeds. Further research is needed on graminoid: forb ratios, invasion resistance, and eventual species diversity of restorations.

Much research has been conducted on how to restore the high levels of plant species and phylogenetic diversity in native grassland systems (Polley et al. 2005, Martin et al. 2005, Barak et al. 2017), with results suggesting that some plant diversity is achievable in restorations, but not to the level of remnant (reference) sites. Our results were consistent with this general finding. Globally, restoration efforts fail to achieve complete recovery to reference communities (Jones et al. 2018) and, in general, restored grasslands have lower richness and diversity than remnants (reviewed in Wilsey 2018).

Effect of seeding method

The type of seeding method may impact establishment outcomes, and some studies have found evidence that broadcasting, rather than drilling seed, results in more diverse restorations (Norland et al. 2015, Applestein et al. 2018). We did not find evidence for this effect, but we did find higher richness of native species in restorations seeded using a combination of seeding and broadcasting compared to a single one. A different set of species may be favored by seeding vs. broadcasting, and using both types may lead to a greater establishment of native species in restorations.

Nonsignificant predictors of restoration success

Some measures that have been proposed to influence plant diversity in restorations, including burn treatments and precipitation during early establishment, did not significantly predict diversity. Fire is a natural disturbance in tallgrass prairie and is also predicted to influence species diversity under the deterministic assembly model, yet somewhat surprisingly, we did not find evidence that fire drives patterns in restoration success. This could have been due to the timing of prescribed burns, which are usually done in spring (March or April) in our area, and the exotic species that were most common. The effects of fire on the common exotic species in our study depend on timing of burns, with fire being ineffective on *Bromus inermis* when applied in April, and not later in May (Blankespoor 1987, Becker 1989, Willson 1992). Fire is also ineffective against *Phalaris arundinacea* (Foster and Wetzel 2005). More research is needed on the most effective timing of fire.

We found plant community composition was more similar to the seed mix with higher establishment precipitation, but other measures of success were not related to precipitation. Variation in early water availability has been experimentally shown to influence seedling establishment in a restored prairie, with greater emergence occurring with more precipitation; however, the strength of this effect is strongly species specific (Groves and Brudvig 2019). The pattern we observed, with higher establishment precipitation increasing community similarity to the seed mix, but not increasing native or total richness, may result if a few seeded species such as grasses (which are proportionally large components of seed mixes) respond more strongly to early precipitation.

Finally, some potentially informative establishment variables that we were unable to account for may be important and deserve further study. Evidence from a seeding experiment using a 128-species mix indicates that, after the first 2 yr of assembly, restorations with higher seeding rates (56 and 78.5 kg/ha) had higher richness and diversity of seeded species compared to a lower rate of seeding (11.2 kg/ha), but it is not clear if these effects are persistent (Goldblum et al. 2013). We were also unable to account for the timing of seeding due to a lack of variation; there is some evidence that spring seedings tend to have higher diversity than fall seedings (Martin and Wilsey 2012).

Conclusions

Prairie restorations were highly variable in their management and outcomes, with most being less diverse and species rich, and with a higher degree of invasion, than remnants. The abundance of exotic species was the best predictor of diversity. Thus, the top priority for prairie management should be control of invasive exotics, especially biennial and perennial species. Targeting restorations for sites with a less abundant exotic seed bank, or where exotics are less likely to disperse, should be an effective way to establish diverse restorations. Previously, a negative relationship between plant diversity and the abundance of exotics has been documented at the plot scale within a restored grassland (Middleton et al. 2010), but here we demonstrate that this trend is characteristic of restored prairies generally. Mowing during the first 2 yr of establishment, and locating restorations in less fertile soils in less linear habitats are all effective strategies to promote more diverse restorations.

Taken together, our results indicate that community assembly in restorations is most consistent with a stochastic/alternate states model, where the diversity of restorations does not converge over time but rather is highly variable and contingent on factors influencing the abundance of exotic species and weather conditions during establishment.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2252/full

Data Availability

Data are available from the Dryad Digital Repository (Kaul and Wilsey 2020): https://doi.org/10.5061/dryad.2547d7wp2